The effect of diets of phytoplankton and suspended bottom material on feeding and absorption of raft mussels (Mytilus galloprovincialis Lmk)

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Abstract

Measurements of feeding rate and absorption efficiency were performed to assess the nutritional value of sedimentary organics combined with phytoplankton for raft mussels (Mytilus galloprovincialis Lmk) in Ria de Arosa (Galicia, N.W. Spain). Both clearance rate and absorption efficiency reached a maximum on mixed diets in which the proportions of phytoplankton and sediment particles were similar. Consequently, maximum absorption rates were reached on laboratory suspensions that closely resembled features of natural seston from the Ria. Values of absorption efficiency recorded with suspended sediments (around 13%) do not apply to the detrital component of ingestion in mixed diets, leading to the conclusion that a positive effect of phytoplankton on absorption efficiency of sedimentary organics is taking place. On the other hand, comparison of results for mixed and monoalgal diets also suggests that the occurrence of silt in the ingesta enhances absorption of microalgae, possibly through improving mechanical treatment within the stomach. It was concluded that mixing of bottom material with phytoplankton in the water filtered by raft mussels greatly increases growth potential, provided that no reduction of phytoplankton concentration below 40% of particulate volume takes place. Mussels with different locations in the Ria exhibit variable degrees of infection by the parasitic protozoa Marteilia refringens. Concomitant differences in physiological behaviour could be attributed to digestive impairment caused by parasitization.

Keywords: Absorption efficiency; Bottom sediments; Feeding; Mytilus; Parasite; Phytoplankton

1. Introduction

Mussels from Galician Rias experience growth rates that rank among the highest recordings: Perez Camacho and Roman (1979) and Perez Camacho et al. (1991) reported a 30-fold increase in initial biomass over seventeen months, a time span when shell length increased from 10 to 80-90 mm. For many years the general consensus was that local upwelling phenomena (Otto, 1975; Tenore et al., 1982) by promoting dense phytoplanktonic blooms, created optimal conditions for bivalve growth. Although very high planktonic primary production (Cabanas et al., 1979; Nunes et al., 1984; Varela et al., 1984) on its own cannot explain the recorded growth rates of mussels. Calculations by Perez Camacho and Gonzalez (1984), based on mean values of primary production in Ria de Arosa (250 g $C.m^2 \cdot yr^{-1}$; Nunes et al., 1984) and filtration rates measured in the laboratory concluded that filtration of phytoplanktonic carbon would amount to only 86% of the total carbon that had actually been incorporated in the mussels culture as based on measurements of growth and reproductive output. Obviously, an additional source of nutrients should be invoked and organic detritus can be considered to play an important role as regards the energetics of these mussels. In fact, when growth efficiencies recorded in Arosa (mean 40%; Navarro et al., 1991) are applied to the above calculations, phytoplankton production explains no more than 35% of mussels' growth. As an indirect confirmation of these figures, phytoplankton biomass estimated from seasonal data of Chlorophyll a (Nunes et al., 1984), represents about 40% of particulate organic matter suspended in the water column during the spring-summer period (mean: 0.6 mg . l^{-1}; Cabanas et al., 1979; Navarro et al., 1991), and probably a lesser fraction in autumn and winter.

Regarding composition of these detrital materials, partly mineralized sediments in the bottom of the Rias are of particular importance as they constitute an extensive reservoir of organic matter available under the action of hydrodynamic factors. In spite of the low organic content of these materials (15 to 20%) and the fact that no organic enrichment, by means of pre-ingestive selection of particles, is possible (seston concentrations in the Rias being typically below the pseudofaeces threshold for Mytilus: Widdows et al.,

1979; Bayne et al., 1993), food availability from sediments is expected to be high. The following considerations are given in support of this expectation:

1. Food quality of bottom materials can be higher than indicated merely by their organic content. According to Bayne et al. (1987) and Navarro et al. (1991) absorption efficiency of Mytilus would be determined by the ratio of organic weight to particle volume (amounting to 0.33 $mg \cdot mm^{-3}$ m. present sediments) rather than the organic content by weight (amounting only to 0.16).

2. Digestibility of refractory organics may be greatly increased by bacterial action. For instance, Stuart (1982) has reported that absorption efficiency in the mytilid Aulacomya ater fed kelp detritus increases with ageing of this material in the presence of bacteria.

3. The occurrence of mineral particles within the ingesta of M. edulis has been considered beneficial by different authors (Winter, 1976; Kiorboe et al., 1980), given its possible grinding function, which would improve the mechanical treatment of food.

Following previous determinations of the scope for growth of cultivated mussels with natural seston (Navarro et al., 1991), the aim of the present series of experiments was to assess the dependence of growth rate on feeding conditions in an environmentally realistic context. For this purpose, features of natural seston were simulated by mixing bottom sediments with phytoplankton and measuring assimilation by mussels fed these suspensions. Diets were designed so that the proportion of the two components was varied, their relative contribution to the energetics of mussels being assessed by this means.

Physiological traits have been reported to exhibit considerable site variability within Ria de Arosa, (Navarro et al., 1991) and transplantation experiments have shown these differences to have an endogenous component (not explained by spatial variability in seston composition) that persisted after two months (Iglesias et al., data not shown). Therefore, mussels from two sites were compared in order to address a possible interaction between such an endogenous component and dietary composition. As to the cause of persistent differences, increasing evidence points to the degree of parasitisation by the protozoa Marteilia refringens, which appears to be highly correlated with the

ingestion rate, absorption efficiency and the condition of the mussels from Arosa (Perez Camacho et al., data not shown). Histological examination of mussels from both sites was thus undertaken in order to establish the levels of infestation by this parasite.

2. Materials and methods

2.1. Collection and maintenance

Mussels from Galician rias have been assigned to the Mediterranean species Mytilus galloprovincialis (Lmk.) (Sanjuan et al., 1990). However, the systematic status of this mussel, whether a distinct species or a subspecies of the larger M. edulis complex, is still controversial (see Gosling, 1992). Specimens of mussels with a shell length measuring approximately 80 mm were collected from two cultivation rafts in the Ria de Arosa (Galicia, N.W. Spain), in November 1990. Raft locations were included within an oceanic-terrestrial gradient and henceforth will be termed sites O (outside) and I (inside). Acclimation to laboratory conditions proceeded for 2 days, with the animals held in feeding tanks with flowing sea water at the environmental temperature (15°C) salinity (35‰) and seston concentration (not determined). Mussels were fed on experimental diets for 12 h prior to, and while undertaking, physiological determinations.

2.2. Experimental diets

Dietary composition included one or both of the following two particulate components: 1) Cells of the alga Isochrysis galbana (clone T-ISO) and 2) bottom sediments which had been taken from underneath the rafts (approx. 10 m depth) and were subsequently freeze-dried. A range of food quality was obtained by mixing up these components according to the following proportions: 100:0 (diet A), 75:25 (diet B), 40:60 (diet C), 25:75 (diet D) and 0:100 (diet E), for the ratio of alga:sediment, as given in terms of particulate volumes measured with a Coulter Counter TA-II, fitted with a 100-μm tube.

The above mixtures were added to sea water filtered from background particles > 1 μm, while it was passed through the experimental tanks, and dosed as to provide the mussels with a constant particle concentration of 1 $mm^3\ l^{-1}$, a value characteristic of Ria de

Arosa in different seasons. For this purpose, the concentration was continuously monitored with a Coulter Counter TA-II and pertinent adjustments of the dosing rates were made. Particulate volume was considered a better reference for food availability than weight or the number of particles, with standardization with respect to volume becoming most important in these experiments where both mean particle size and density were highly variable among the diets.

Characteristics of diets are given in Table 1, where a quoted value represents a mean (± S.D.) of five water samples taken over the experimental period from the feeding tanks in the proximity of animals. For weight determinations of total particulate matter (TPM) and particulate organic matter (POM), water samples were filtered onto pre-ashed (450°C for 4 h) and weighed GFC filters, rinsed with sea water-isotonic ammonium formate and dried at 110°C. The dry weight of retained material gave the TPM and the weight loss on ignition at 450°C gave the POM. Total particulate volumes (VOL) were obtained by counting particles in the range of 3 to 50 μm with a Coulter Counter TA-II. Two indices of food quality were used in this work: organic content by weight (= POM/ TPM) and by volume (= POM/VOL).

2.3. Physiological measurements

Physiological components of absorption were determined as follows:

a) Clearance and ingestion rates: Clearance rate was individually estimated (n = 5) in a closed, 3 1 system, by recording the exponential decline of particles > 3 μm and < 60 μm, measured with a Coulter Counter TA-II (Coughlan, 1969). The ingestion rate was determined as the product of clearance rate and particle concentration.

b) Efficiencies and rates of absorption: Pooled samples of faeces (n = 5) from each of two individuals were filtered on GFC filters and processed for total and organic dry weight of particulate matter, as described in Section 2.2. Replicate samples were taken three times over 16 h of experimentation. Absorption efficiency was computed from the organic content of food and faeces, according to the method of Conover (1966). The absorption rate was then calculated as the product of organic ingestion and absorption efficiency.

2.4. Size-standardization of physiological rates

After physiological determinations were concluded, shell lengths were measured to the nearest mm, soft tissues of each animal being excised, dried at 85°C and weighed. For reasons that are not discussed here (Iglesias et al., data not shown), shell length is a size-parameter more convenient than soft body dry weight for clearance rate standardization, when large variability in the condition index occurs. Consequently, individual clearance rates were standardized to an equivalent 80 mm shell length using the formula adapted from Bayne and Newell (1983):

$CR_e = CR_e(80/L_e)^h$

where CR_e and CR_e are the standard and uncorrected clearance rates, respectively, L_c is the shell length of experimental mussels and b is the power that scales the clearance rate with the shell length in mussels from Arosa (b = 1.85; Perez Camacho and Gonzalez, 1984). No size-standardization is required for absorption efficiency (Bayne and Newell, 1983).

2.5. Parasitization

Samples from the stomach and digestive gland of some 30 mussels per site were processed for histological analysis according to the method of Villalba et al. (1993). One histological section from each mussel was examined under a light microscope, to assess the occurrence of Marteilia refringens (Grizel et al., 1974). The intensity of infection was quantified following procedures described by Villalba et al. (1993), where each mussel is rated according to its level of infection, on a scale from 0 (uninfected) to 5 (heavily infected). A mean incidence for each group is then computed as the product of the number of mussels in each level by the corresponding value on the scale, divided by the total number of mussels.

3. Results

3. 1. Diets

While designing the diets, a prime interest was to standardize particle concentration to 1 $mm^3 . l^{-1}$. Data from Table 1 shows a marked departure from this value for diet E (pure sediment), a moderate one for diet A (pure phytoplankton), but good agreement for diets B, C and D, the composition of which most closely represented natural seston. Additionally, no great differences existed among these three diets in terms of organic concentration (POM) and hence quality (POM/VOL). Despite this uniformity, there were great differences in composition: Phytoplankton represented actually 75, 41 and 27% of total particulate volume (compared with aimed values of 75, 40 and 25%) and 87, 71 and 58% of particulate organic matter in diets B, C and D, respectively.

3.2. Clearance rates

Fig. 1 shows clearance rates (CR) of standard-sized mussels from rafts in the I and O areas of the Ria de Arosa. Dietary composition has a definite effect on clearance rate of mussels from both sites.

Maximum values were recorded in response to mixed diets, where the algal component constitutes 30 to 40% of total particulate volume. This is similar to the natural abundance of phytoplankton in seston of the Ria.

Superimposed on dietary effects are site differences represented by higher values of CR in mussels from site O. According to results from a two-factor ANOVA (Zar, 1984) (Table 2) both diet and site exert significant and independent (see lack of significance of interaction term) effects on CR. Present CR values used in ANOVA were standardized to shell length; however, the same results from ANOVA treatment were obtained with CR values standardized to dry weight.

3.3. Absorption efficiency

For mussels from site O, absorption efficiency (AE) was held relatively constant (around 60%) on phytoplankton and mixed diets, but decreased to 12% on a sediment diet (diet E in Fig. 2). A similar decreasing trend with reducing food quality is noticeable in mussels from site I, but in this case, increasing quality above a certain level also reduces AE, which results in a maximum with diet C.

As for CR, two-factor ANOVA showed a significant influence of both site and diet (Table 3a). In this case, however, effects were inter-dependent (interaction term was highly significant), as clearly indicated in Fig. 2 by large differences between sites when high quality diets, especially diet A, are used. In fact, when AE data measured with diet A were omitted in ANOVA analysis (Table 3b), the effects of site lost significance and site-diet interaction was only marginally significant. Thus, with the exception of reduced AEs recorded with diet A in mussels from the inner area, most variability in AE could be explained in terms of dietary composition.

According to previous treatments, AE of Mytilus can be conveniently expressed as a function of food quality (Q), this given as POM per unit particulate volume (POM/VOL) (see Section 1). Theoretically, the form of this relationship would be a hyperbola, based on the following assumption that applies to the digestive physiology of Myths: Gross absorption and metabolic faecal losses would constitute constant fractions of organic and total ingestion, respectively (Bayne and Hawkins, 1990; Hawkins et al., 1990). Accordingly, an expression for this relationship in mussels from Arosa was obtained by fitting an extensive set of data of AE vs. Q (Navarro et al., 1991; Iglesias et al., data not shown) with a linear regression, preceded by inverse transformation of the independent variable to linearize the hyperbolic trend (Fig. 3). When present data (with its 95% C.I.) are plotted on this regression line, it becomes clear that AEs recorded in this work are not significantly different from predictions based on this relationship, with the exception of mussels from site I fed the monoalgal diet A.

3.4. Absorption rate

Absorption rates (AR) are the product of food availability (POM concentration), CR and AE. While AR appeared to be highly correlated with CR and AE ($P = 10^{-4}$), there was no significant correlation with POM ($P > 0.2$). This means that the magnitude of energy gain by raft mussels is determined through physiological adjustments rather than being dependent on food availability (see also Navarro et al., 1991).

Maxima clearance rates were recorded with diets where phytoplankton represented between 25 and 50% of the total particle volume, and these diets were also absorbed

with the highest efficiencies, thus resulting in peaks of absorption in that range of composition. Fig. 4 shows absorption rates standardized to a constant particle concentration of 1 $mm^3 \cdot l^{-1}$ (the aimed value in these experiments) as a function of the composition of the diet (organic content and phytoplankton abundance). In both groups of mussels absorption reached a maximum with diet C (≈ 40% of both organic content and abundance of Isochtysis), and declined with increasing or decreasing quality. There is some departure from this trend with monoalgal diets, where a maximum difference in absorption between groups of mussels is mainly caused by differences in AE.

3.5. Parasitization

Table 4 gives the number of mussels presenting different stages of infection by Marteilia refringens for sites O and I. A value of 20% of mussels from site O showed some level of infection and mean incidence of the parasite, computed according to Villalba et al. (1993), was 0.30 in this group. As for site I, infection was recorded in 53% of mussels with a mean incidence of 0.90.

4. Discussion

Mixed diets assayed in this work (B, C and D) cover the range of seasonal and site variability in seston characteristics in Ria de Arosa (Cabanas et al., 1979; Navarro et al., 1991; Iglesias et al., data not shown). Consequently, conclusions drawn from the study of the experimental diets are relevant to prevailing environmental conditions.

Since the beginning of this decade (Jorgensen, 1990), features of feeding behaviour of bivalve molluscs, particularly those concerning pumping and clearance rates, may receive two alternative interpretations: They may either be considered as components of the organism's fitness in variable food environments or regarded as fortuitous, at best reflecting variable degrees of "environmental adversity" (sic) (see Jorgensen, 1990; p. 66). In this respect, it becomes appropriate to declare our preference towards the first kind of interpretation by stating that present physiological results will be discussed on the grounds of optimality principles. According to such principles, modifications of feeding behaviour in response to changing dietary conditions, as reported here, are regarded as functional adjustments achieving maximum energetic benefit, taking

account of constraints imposed by characteristics of the alimentary-digestive system of bivalves. These constraints mostly relate to digestive processes (see Bayne et al., 1993; Navarro et al., 1994) and underlies the behaviour of AE (Navarro and Iglesias, 1993).

For mussels from site 0, AE was reduced with decreasing quality, reflecting the fact that metabolic faecal losses become a greater fraction of the organic ingestion in diets of low organic content (Bayne and Hawkins, 1990). This interpretation applies to mussels from site I as to the series of diets C-D-E; conversely, there is no immediate explanation for the decline in AE with increasing organic content in this group of mussels, following the series C-B-A. M. refringens proliferates inside the digestive epithelium and is likely to impair digestive processes. Consequently, levels of infection that are three times higher in mussels from site I, are likely to result in greatly reduced gut capabilities. Nevertheless, such a limitation only becomes apparent with diets A and B, i.e., when organic ingestion exceeds a certain level or, alternatively, the mineral component of the diet, which might improve the mechanical treatment of food within the stomach, is scarce or lacking. Whatever the factor responsible for this phenomenon, it does not appear to play any role in less parasitized mussels from site O.

Active feeding response of mussels to changing composition of food is represented by CR variation by a factor of ca. 2.5. All diets considered together (i.e., across food qualities), there is a positive relationship between AE and CR. This result suits the above optimization principles, given that: 1) as increasing ingestion tends to reduce the gut passage time of food, it is only with easily digested and absorbed diets (i.e., high AE) that an organism could maximize return from enhanced clearance and ingestion rates and 2) a more efficient digestive process would create more space inside the gut that would be available for ingestion. Composition of diets C and D would be most appropriate in this respect, allowing great amounts of ingested food to be processed with high efficiency. This results in maximum energy gain with these diets, which more closely resemble natural seston in Ria de Arosa.

To fully understand the basis for these suspensions having an optimal composition, it would be most interesting to be able to separately computing AE of phytoplankton and detritus when both components of the particulate organic matter are ingested together, as in mixed diets. Requirements for such a calculation are not fulfilled by the conditions

of present experiments. However, several approaches can be envisaged: For example, by assuming that retention by the gill does not modify the recorded proportions of both components in food suspensions, calculation of rates of Isochrysis and detritus ingestion becomes possible in individual mussels. AEs measured with diet E, which is supposed to represent the AE of organics in sediments, were applied to the detritic component of ingestion in mixed diets, to compute the absorption coming specifically from this nutritional source. Next, this component of absorption was substracted from the total absorption, to estimate the absorption rate from 1sochrysi.s. Figures for AE of phytoplankton, obtained by dividing these absorption rates by the ingestion rates of the algae, exceeded 100% in most cases. This indicates that AEs for diet E were not in fact applicable to the detritic component in mixed diets and lead to the conclusion that the presence of phytoplankton in the ingesta increases the AE of sedimentary organics with respect to diets where sediment is the sole constituent. Bayne and Hawkins (1990) have reported induction of carbohydrase activities following acclimation of M. edulis to increased phytoplankton abundance in the diet, so that a change in the level of digestive enzymes could be invoked to account for the present improvement in digestive function. Although no analysis have been undertaken in the case of mussels in the short-term, there is evidence of a two-day response in the digestive gland of the cockle Cerastoderma edule (Ibarrola et al., 1994).

Quantitative assessment of the increment achieved in the AE of detritus for mixed diets is difficult, although some assumptions are possible. For example, one assumption could be that the algal component in mixed diets would be processed similarly to that in monoalgal diets. On this basis it becomes possible to compute AEs for the microalgal fraction in mussels ingesting mixed diets and subsequently these values could be used to estimate AE for the detrital fraction according to procedures explained earlier. One important relationship governing digestive processes of bivalves is the exponential decrease in AE with increasing ingestion rate, which is particularly noticeable with monoalgal diets (Thompson and Bayne, 1974; Widdows, 1978; Griffiths and King, 1979). When mussels are fed Isochrysis exclusively (Diet A), inter-individual variability in ingestion rates is quite large (x 4), affording the possibility of checking such a relationship. Indeed, correlations between individual values of AE and organic ingestion (log, transformed to account for the exponential dependence) were significant with diet A (group 0: $P = 0.01$; group I: $P = 0.02$); whereas, no such correlation was

found with sedimentary organics (i.e., with diet E; P = 0.2 for mussels from both sites). Accordingly, expressions describing the behaviour of AE as a function of Isochrysis ingestion were developed to predict AEs of the algal component in the mixed diets, and were used to compute the AE of the sedimentary component Fig. 5. shows exponential functions of the form $AE = e^{-blR}$, fitted to both sets of AE data with diet A for mussel groups 0 and I, together with similar relations reported in the literature for M. edulis (Thompson and Bayne, 1974; Widdows, 1978).

Absorption efficiency of sedimentary organics, computed by using AEs for phytoplankton obtained through relationships given in Fig. 5, are presented in Table 5a. No account of any mechanical effect of silt on algal AE is given in these calculations and values in Table 5 could in fact constitute an overestimation; however, in no case would this effect explain the great differences found with respect to diet E.

A two-factor ANOVA (Table 5b) concluded lack of significant differences associated with site, but differences among diets were highly significant. Multiple comparison procedures (LSD test; Sokal and Rohlf, 1981) revealed that diet B was significantly different from diets C and D, thus leading to the conclusion that lack of homogenity comes from reduced values of detrital AE with diet B, where silt was comparatively scarce. This finding adds weight to the idea that mineral particles are beneficial for digestion in Myths.

In summary, composed diets based on phytoplankton and bottom sediments that reproduce features of natural seston of the Ria de Arosa appear to represent optimal nutritional conditions for mussels, as these suspensions bring about the greatest rates of absorption. Results reported here indicate that the occurrence of phytoplankton in the ingesta induces more active absorption of detrital organics. Besides, there is evidence pointing to a positive influence of sediment on digestion and absorption of microalgae, based on a possible auxiliary role of silt particles regarding the mechanical function played by the crystalline style. Consequently, natural sediments suspended in the water column would greatly promote absorption and hence growth of cultivated mussels, provided that no reduction of phytoplankton abundance below 40% of the total particulate volume takes place. The results also suggest that moderate levels of infection by M. refringens should have no adverse effect on feeding, absorption and growth rates

of mussels when fed mixed diets; however, the situation might dramatically change should phytoplankton become the predominant or exclusive component of seston.

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Table 1

Characteristics of diets

Diet	TPM ($mg.l^{-1}$)	POM ($mg.l^{-1}$)	VOL. ($mm^3.l^{-1}$)	Quality	
				(POM/TPM)	(POM/VOL)
A	1.01±04	0.93±0.06	1.43±0.14	0.91±0.03	0.65±0.03
B	0.83±0.07	0.46±0.03	1.00±0.04	0.56±0.01	0.46±0.05
C	1.18±0.08	0.44±0.03	0.95±0.10	0.38±0.02	0.48±0.07
D	1.58±0.23	0.47±0.02	1.16±0.25	0.30±0.04	0.42±0.10
E	3.71±0.26	0.60±0.06	1.88±0.31	0.16±0.02	0.33±0.07

TPM = total particulate matter; POM = particulate organic matter; VOL = total particulate volume l^{-1}.

Two indices of food quality are presented; the organic content by weight (POM/TPM) and by volume (POM/VOL).

Quoted values are means ±S.D.

Table 2

Results of two-factor ANOVA for testing significance of differences between clearance rates of Mytilus galloprovincialis from sites (outer and inner) within the Ria de Arosa

Factor	d.f.	ss	MS	F	P
Diet	4	75.35	18.84	10.83	10^{-4}
Site	1	13.22	13.22	7.60	0.009
Interaction	4	13.03	3.26	1.87	0.134
Error	40	69.59	1.74		

Table 3

Results of two-factor ANOVA for testing significance of differences among absorption efficiencies of Mytilus galloprovincialis from sites (outer and inner) within the Ria de Arosa

Factor	d.f.	SS	MS	F	P
a) All diets					
Diet	4	1.52	0.38	75.41	10^{-4}

Site	1	0.05	0.05	10.08	0.003
Interaction	4	1.77	0.04	8.76	10^{-4}
Error	40	0.20	0.05		
b) Without diet A					
Diet	3	1.52	0.51	222.36	10^{-4}
Site	1	0.001	0.001	0.27	0.608
Interaction	3	0.02	0.007	2.96	0.047
Error	32	0.07	0.002		

Table 4

Intensity of infection by the parasite Marteilia refringens of mussels Mytilus galloprovincialis from sites (outer and inner) within the Ria de Arosa

Level of infection	No. of infected mussels	
	Site O	Site I
0	24	14
1	4	9
2	1	4
3	1	2
4	0	1
5	0	0
Mean incidence	0.3	0.9

Intensity of infection was quantified according to Villalba et al. (1993) (see Section 2)

Table 5

a) Absorption efficiencies of sedimentary organics from mixed diets by Mytilus galloprovincialis, estimated as described in the text. Quoted values are means ±95% C.I.

b) Results of two-factor ANOVA for testing significance of differences among these values

a)		
Diet	Site	
	O	I
B	0.216±0.110	0.296±0.251
C	0.558±0.042	0.607±0.057

D			0.451±0.050		0.516±0.046
b)					
Factor	d.f.	SS	MS	F	P
Diet	2	0.557	0.279	21.05	10^{-4}
Site	1	0.033	0.033	2.47	0.13
Interaction	2	0.001	5×10^{-4}	0.04	0.96

Fig. I Clearance rates of standard-sized Mytilus galloprovincialis measured with diets A (phytoplankton), B, C, D (mixed) and E (sediment). Left columns, site O; right columns, site I. Values are means ±95% C.I.

Fig. 2. Absorption efficiencies of Mytilus galloprovincialis measured with diets A (phytoplankton). B, C. D (mixed) and E (sediment). Left columns, site O: right columns, site I. Values are means ±95% C.I.

Fig. 3. Regression line of AE vs. 1/Q (Q = mg POM/mm^3) fitted to previous measurements in Ria de Arosa (Navarro et al., 1991; Iglesias et al., data not shown). Points are data from the present work (means+95% C.I.). Full circles, site 0; hollow circles, site I.

Fig. 4. Rates of absorption by Mytilus galloprovincialis as a function of organic content and Isochrysis abundance (5%). Values (means-+95% C.I.) standardized to a constant particle concentration (= 1 mm^3 l^{-1}).

Fig. 5. Absorption efficiency of Mytilus gulloprovincialis as a function of the ingestion rates of phytoplankton. Continuous lines: Results of fitting present data for monoalgal diets (A) with an exponential equation of the form: $AE = e^{-hIR}$. Site O, b = 0.168±0.056; Site I, b = 0.732±0.227 (295% C.I.). Differences among b values were found to be highly significant: t = 8.19; $P < 0.001$ (Zar, 1984). Dotted lines: Similar relationships reported for Mytilus edulis by Thompson and Bayne (1974) (line I) and Widdows (1978) (line 2).